

ADVANCED (CONSTANT) INSECT POLLINATION MECHANISMS: PATTERN OF EVOLUTION AND IMPLICATIONS VIS-À-VIS ANGIOSPERM DIVERSITY¹

WILLIAM L. CREPET²

ABSTRACT

The functional/phylogenetic relationship between the angiosperm flower and insects, combined with the correlation between insect pollination and many of the most diverse angiosperm families, suggest that insect pollination has had an important role in angiosperm success. Various advantages of insect pollination at the species level, especially those associated with bee and lepidopteran pollinators, are consistent with these correlations—furthermore, modern angiosperm diversity may be more directly related to insect pollination by the speciation-promoting characteristics of constant pollinators. Until the present time, paleontological data have mitigated against this possibility by illustrating that both advanced insect pollinators and their co-adapted angiosperm flowers evolved too late to have been of major significance in angiosperm radiation. Recent analyses of paleobotanical and biogeographical data together with paleobotanical data indicate that hymenopteran and lepidopteran pollinators, and angiosperm taxa having flowers adapted to them, existed at a time of major angiosperm radiation. Although angiosperm success cannot be confidently related to one feature, the importance of insect pollination in the diversification of the group can no longer be minimized in the context of the fossil record. Angiosperms are distinguished among the tracheophyta by their overwhelming diversity [250/300 families of vascular plants are angiosperms; 240,000/300,000 species of flowering plants are angiosperms (Burger, 1981)]. The angiosperms are also dominant in sheer numbers of individuals and are of extraordinary economic importance. Furthermore, angiosperms demonstrate stunning variation in vegetative and reproductive morphology, anatomy, and habit.

Attempts to explain angiosperm diversity might be directed logically at explaining the potential benefits of unique, basic angiosperm features (i.e., synapomorphic features at the level "Angiospermae"). These are dominated by characters related to floral morphology and function including the hermaphroditic condition, enclosed ovules, monosulcate granular-walled pollen, double fertilization, and insect pollination. Angiosperm flowers are related to insect pollination by functional morphology and phylogeny and they are probably the products of co-evolution with insects (e.g., Grant, 1950; Crepet, 1979; Stebbins, 1981). There are numerous examples of radiations in angiosperm taxa associated with adaptations for various animal pollinators (e.g., the Polemoniaceae, Grant & Grant, 1965), especially faithful pollinators, and particularly the Apoidea (bees). The Apoidea may be temporally (polytropic—a tendency to pollinate one species at a time) or more or less ab-

solutely (oligotropic-monotropic) faithful, and flowers may be adapted to bee (and other) pollinators in a variety of ways (Heinrich, 1979, 1981; Macior, 1974). Correlations between various diverse angiosperm taxa and animal pollinators, particularly constant pollinators, suggest that there may be a fundamental relationship between animal pollination and diversity (Grant, 1949; Grant & Grant, 1965; Baker & Hurd, 1968; Crepet, 1979). Certain aspects of insect pollination may include characteristics that provide competitive advantages to insect-pollinated taxa as well as those more immediately related to speciation (and the production of diversity).

At the species level, these include:

- a. Reliable directional pollination with its energetic advantages (Pohl, 1937; Cruden, 1977).
- b. The production of outcrossed offspring in a population of relatively widely dispersed individuals (Burger, 1981).

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² Biological Sciences Group U-42, University of Connecticut, Storrs, Connecticut 06268.

- c. Successful pollination under environmental conditions inappropriate for wind pollination.

Potential advantages at the level "Angiospermae" (i.e., those related directly to diversity) include:

- a. The filling of "empty" niches as a result of "b" and "c" above.
- b. The deflection of faithful pollinators from their host plant through stochastic change in key floral features (altered developmental patterns) could provide the means for restricting gene flow from parental populations to isolated (peripheral or sympatric) demes (see the scenarios outlined in Fig. 1A and B based on Grant, 1949; Gottlieb, 1982; Tiffney, 1984).

The combination of these features of angiosperm reproductive biology represents a mechanism for increasing the frequency of the formation of small, genetically isolated populations in which evolution can proceed rapidly (due to founder effect/drift, the potentially rapid fixation of mutations, etc.), thus maximizing the probability of speciation and conforming with the punctuated equilibria model of Eldredge and Gould (1972) and Gould and Eldredge (1977). The net result: augmented speciation in angiosperms consistent with their present diversity (Fig. 1).

Many features of the angiosperms can be reasonably regarded as having contributed to their present diversity. For example, Mulcahy has considered the advantages conferred by a reproductive system that allows for gametophytic as well as sporophytic competition (1979) and Tiffney (1984) pointed out the speciation-promoting quality of having animal dispersed seeds (see also the discussion below and Crepet, 1982). Burger (1981) and Stebbins (1981) have independently summarized and evaluated the various features of angiosperms likely to have been important in their present success. Stebbins pointed out the need to consider the fossil record in assessing the impact of insect pollination on present angiosperm diversity. He noted that the types of pollinators most likely to be directly involved in the establishment of diversity (i.e., constant pollinators) evolved too late to have participated in major angiosperm radiation and considered insect pollination to have been supplemental, and

not essential. Stebbins (1981) considers attributes he views as following from the reduction of the female gametophyte as having been of major significance in angiosperm success. These include the closed carpel, double fertilization, and the styler canal. Few would debate the potential advantages of these features (the ultimate role of the carpel, for example, in fruit dispersal), but Stebbins's implicit separation of these characters from co-evolution with insect pollinators is open to question.

More recent paleontological and neontological information suggests an alternative interpretation of the timing of the evolution of constant pollinators and of the radiation of the angiosperms. It is my intention to offer a preliminary account of the diversification of advanced adaptations to insect pollination likely to have involved constant pollinators and of the possible implications with regard to angiosperm history. The bases for my argument include:

1. The growing fossil record of flowers, inflorescences, and fruits.
2. Bee biogeography and its evolutionary significance, as recently discussed by Michener (1979).
3. Recent data on patterns of diversification in the angiosperms (e.g., Niklas et al., 1980; Muller, 1981; Tiffney, 1981).
4. Improved understanding of the taxonomic value of pollen and leaves combined with growing information on the occurrences and states of different organs representing the same taxa from the same localities or times.

PALEOBOTANICAL EVIDENCE ON THE STATUS OF ADVANCED POLLINATION

Angiosperms with floral morphology indicative of pollination by advanced constant animal pollinators are conspicuous by the Middle Eocene. Appreciation of the past diversity of these taxa has increased recently because of the growing fossil record of flowers and fruits combined with a better understanding of the taxonomic significance of fossil leaves and pollen.

Flower and inflorescence fossils have been important in assessing the status of families with advanced pollination mechanisms at various times in the past. They provide the details of floral morphology that can be used, with proper cautions, to infer pollination mechanisms. Floral data have also been important in confirming the

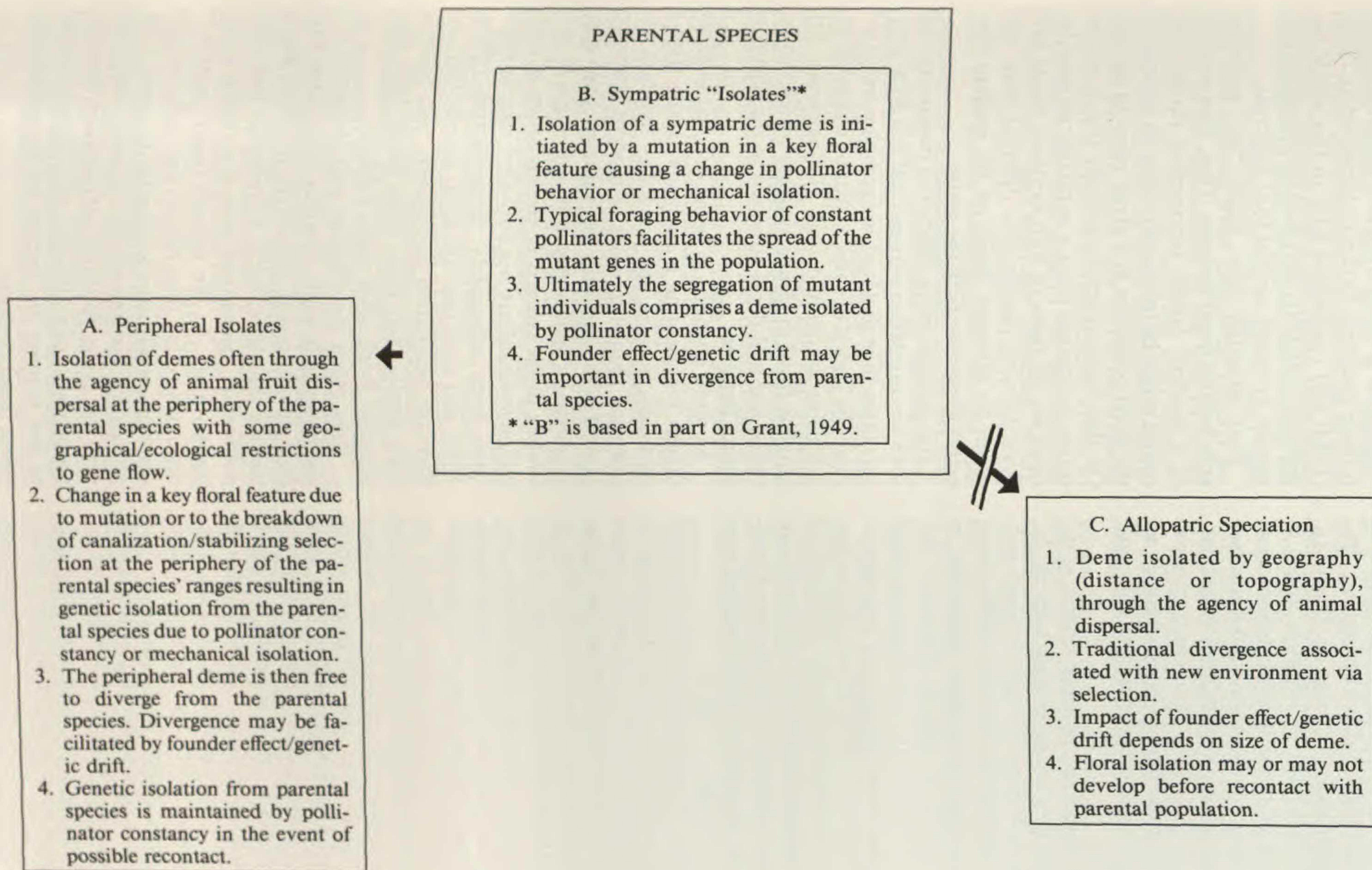


FIGURE 1. Several possible scenarios for the isolation of small populations due to the combination of faithful pollinators, stochastic floral change, and animal seed dispersal.

existence of taxa or of floral character complexes at times when most modern paleobotanists would be reluctant to risk inferring their presence on the basis of other organ evidence alone (e.g., Paleocene Gentianaceae, Crepet & Daghljan, 1981a). Floral data have, in addition, added to the significance of the dispersed palynological record by allowing an assessment of the accuracy with which particular palynomorphs reflect particular suites of associated floral characters and by increasing the taxonomic significance of associated palynomorphs that have been enigmatic when dispersed.

Increasing numbers of in-depth studies of the pollen of extant taxa in conjunction with the increased number of characters used to classify pollen based on scanning electron and transmission electron microscopy have been important in making fossil pollen a valuable diagnostic feature. Fossil leaf studies have also been important in improving our understanding of angiosperm history. Careful studies of leaves have shown that they too may be good taxonomic characters if fine venation patterns and/or cuticular details are determined and analyzed in the context of variation in similar features in extant related taxa (Hickey, 1973; Dilcher, 1974).

A significant problem in interpreting the fossil record of angiosperms has been attempting to deduce the character state of one particular organ from another more commonly preserved organ, in this case, floral structure from pollen, fruit, or leaf evidence. While one character state can never be predicted from another with absolute certainty, neontological data and increasing knowledge of the various organs of particular taxa from specific geological horizons suggest that in recognizably modern families there is a high degree of correlation among the states of the various organs of a taxon [e.g., the Ulmaceae where Eocene celtidoid flowers and pollen both seem reflective of an insect-pollinated ancestry for the now wind-pollinated taxon (Zavada & Crepet, 1981); the Araceae (Crepet, 1978; Dilcher & Daghljan, 1977); the Juglandaceae (Crepet et al., 1975; Manchester, 1981); the Fagaceae (Crepet & Daghljan, 1980; Jones, 1979), etc.].

In certain cases, correlation might be expected. There is a strong functional relationship, for example, between floral and pollen structure that probably extends even to incompatibility mechanisms and pollen ultrastructure (Zavada, unpubl. data). Both flowers and pollen must be adapted to the physical and behavioral charac-

teristics of biotic pollinators or to various physical agencies that might effect pollination. The correlation between fruits and flowers in the past is more complex. Evidence presented by Tiffney (1984) and considered later in this article suggests the possibility that faithful pollinators temporally preceded animal fruit dispersal.

Fruit structure, then, might "lag" evolutionarily behind floral features. Thus, fruit structure of a modern family represented in the fossil record might be too conservative an indicator of the floral condition at a given point in the past. On this basis, it seems unlikely that a modern taxon recognized from a particular geologic horizon on the basis of fruit evidence would have floral features significantly different from what might be expected based on the modern characters circumscribing the taxon.

It is perhaps more difficult to imagine the reasons for correlation between leaf and floral structure other than that both are complex organs and might be united to some extent by character correlations associated with cladogenesis. Yet, growing fossil evidence suggests correlation between leaf and floral structure in the history of extant families.

As more attention is being devoted to all the organs representing a particular taxon from a particular horizon, the possibility that taxa representing unique mosaics of modern characters existed in the past may be evaluated. Such combinations, if sufficiently different, might be misleading in the context of the evolution of pollination mechanisms, but only a few such instances have been adequately demonstrated (Crane, 1982) and in no case has floral morphology, and therefore pollination mechanism, been found to vary significantly from what might have been expected from other organ evidence.

Thus, when the affinities and characters of a particular sufficiently complex organ taxon have been demonstrated *adequately*, it is fairly safe to assume that basic floral morphology and likely pollination mechanism were at a similar evolutionary state. In the present paper, reports of organ taxa other than flowers and inflorescences are occasionally used to infer the presence of the pollination mechanism that is today associated with that taxon. In almost all instances, however, the existence of pollination mechanisms implied in this manner are backed up by contemporaneous floral evidence.

The paleobotanical data. Methods. Two major sources of data other than discrete reports

and work in progress were used in assessing the record of angiosperms with advanced pollination syndromes (Muller, 1981; Reid & Chandler, 1933). These were selected because of the proven taxonomic value of pollen and fruits, their likely correlation with floral structure, and because the quality of the identifications is high in each case. Data were selected from individual reports according to the significance of the taxa involved and only if the reports involved clear demonstration of affinities on solid morphological-anatomical grounds. More data on the occurrences of advanced families will doubtlessly come to light in the future and some of the taxa reported in Muller (1981) and Reid and Chandler (1933), even as modified by Chandler (1961), may not stand up to further investigations, but the data presented are a reasonable state of the art representation of the occurrences of various floral characters at various times in the past.

Data. Table 1 is a summary of all data on the occurrences of families with pollination syndromes typical of the Apoidea and Lepidoptera and even some birds/bats. Families with appropriate syndromes are listed chronologically (however, see footnote a, Table 1) and families may be listed more than once to include as many reliable reports as possible based on as many different types of fossil evidence as possible. The table includes the ages, order, family, type of fossil evidence, characters related to the advanced syndrome and type of syndrome, and pollinators usually associated with the family.

Before summarizing the pattern of evolution of various pollination syndromes, I would like to discuss the appearances of several individual taxa: the Fabales, Asteridae, Zingiberales, and Euphorbiaceae. In these instances, evidence for the appearances of certain character complexes is extremely good and the order and timing of the appearances of the features represented by these taxa serves to corroborate the general impression of the evolution of advanced pollination syndromes gained from Table 1.

Fabales-Mimosaceae. Mimosoids have brush-type blossoms and are pollinated by a variety of faithful pollinators including bees, lepidoptera, and bats. Brush-type blossoms are common in Middle Eocene Claiborne deposits (Fig. 2) and inflorescences similar to modern racemose mimosoid inflorescences are known from the Middle Eocene and younger deposits of the southeastern United States (Crepet & Dilcher, 1977; Daghljan et al., 1980). Spicate inflores-

cences are 6 cm in length with sessile, alternate, perfect flowers (Fig. 3). Floral envelopes consist of a lobed calyx and a corolla with four ovate lobes (Crepet & Dilcher, 1977). There are eight exerted stamens with bilocular, versatile, longitudinally dehiscent anthers (Crepet & Dilcher, 1977). The gynoecium consists of a single carpel with an elongate, pubescent style (Fig. 4). Pollen is borne in tetrads and is tricolporate (Fig. 5).

These inflorescences are very similar to those of modern mimosoids, but subtle palynological differences suggest that they represent an extinct genus. Floral structure and palynological configuration (i.e., why invest units of pollen grains rather than single grains in unfaithful pollinators), suggest that the Eocene mimosoids were also pollinated by faithful pollinators, implying a prior history of co-evolution. Recent discoveries of Paleocene mimosoids support this possibility (Table 1).

Fabales-Caesalpiaceae. While Paleocene inflorescences are the first reliable reports of the Mimosaceae, the Caesalpiaceae have been reported as early as the Maestrichtian on the basis of highly distinctive *Sindora* pollen (Table 1). The presence of the Caesalpiaceae and of myrtaceous pollen (Table 1) in the Maestrichtian also suggests that the brush-type blossom, or one that closely approximates it, originated rather early.

Fabales-Papilionaceae. Studies of paleocene flowers now in progress reveal that the typical highly derived zygomorphic papilionaceous flower already existed at that time. Details will be presented in a subsequent publication (Crepet, unpubl. data).

Asteridae. A recently discovered flower from the Lower Eocene of the Gulf Coastal Plain has several important implications with regard to the tempo of evolution of bee pollination. Flowers are distinctive in having an open, funnelform, sympetalous, seven-parted corolla (Fig. 6) and unusual pollen (Fig. 7). Pollen preserved within compressed anthers is 22 μm in diameter, intectate, triaperturate, and has prominent gemmae (Figs. 7, 8). Pollen is well known as the dispersed Upper Cretaceous-Eocene palynomorph, *Pistillipollenites macgregorii*. Pollen is most common in the Paleocene-Lower Eocene.

The combination of floral and palynological features is suggestive of affinities with the modern Gentianaceae although the taxon is clearly extinct. Floral structure is typical of bee pollination (e.g., Faegri & van der Pijl, 1971) in the angiosperms in general and in the Gentianaceae

TABLE 1. Summary of evidence related to the geological occurrences of angiosperms associated with advanced pollinators.

Subclass	Order	Family	Evidence	Geography	
Upper Eocene					
Asteridae ^a	Gentianales	1. Apocynaceae	1. <i>Rauwolfia</i> -type pollen	1. a) Cameroon b) Venezuela ^b	
	Rubiales	2. Rubiaceae	2. <i>Gardenia</i> -type pollen	2. Germany	
Rosidae	Fabales	3. Mimosaceae	3. <i>Acacia</i> -type pollen	3. Cameroon	
		4. Mimosaceae	4. <i>Adenanthus</i> -type pollen	4. Cameroon	
		5. Mimosaceae	5. <i>Calpocalyx ngnouniensis</i> -type pollen	5. Cameroon	
	Myrtales	6. Mimosaceae	6. <i>Parkia</i> -type pollen	6. Cameroon	
		7. Combretaceae	7. <i>Terminalia</i> -type pollen	7. Cameroon	
		8. Lythraceae	8. <i>Crenea</i> -type pollen	8. Northern South America	
		9. Escalloniaceae	9. <i>Quintinia</i> -type pollen	9. New Zealand	
	Rosales	10. Loranthaceae	10. <i>Amylothea</i> -type pollen	10. New Zealand	
	Santalales				
	Middle Eocene				
Asteridae	Dipsacales	11. Caprifoliaceae	11. <i>Viburnum</i> -type pollen	11. France	
	Scrophulariales	12. Bignoniaceae	12. <i>Dolichandrone</i> -type pollen	12. Southeastern United States	
	Solanales	13. Convolvulaceae	13. <i>Merremia macrocalyx</i> -type pollen	13. a) Brazil b) Nigeria	
Rosidae	Euphorbiales	14. Euphorbiaceae	14. a) <i>Paleowetherellia</i> fruit b) Hippomanean flowers	14. a) Egypt b) Tennessee	
		15. Caesalpiniaceae	15. <i>Brachystegia</i> -type pollen	15. Nigeria	
	Fabales	16. Mimosaceae	16. <i>Eomimosoidea plumosa</i> floral, pollen	16. Texas	
		17. Mimosaceae	17. <i>Pentaclethra macrophylla</i> -type pollen	17. Cameroon	
		18. Myrtaceae	18. <i>Eugenia</i> -type pollen	18. Tennessee	
	Myrtales	19. Malpighiaceae	19. <i>Brachypteris</i> -type pollen	19. Brazil	
	Polygalales	20. Sapindaceae	20. <i>Diplopeltis huegelii</i> -type pollen	20. Central America	
	Sapindales	Zingiberales	21. Heliconiaceae	21. a) Heliconiaceae flowers b) Heliconiaceae leaves	21. a) Tennessee b) Deccan Intertrappean
			22. Musaceae	22. Musaceous fruits	22. Deccan Intertrappean
		Zingiberidae	23. Zingiberaceae	23. Zingiberaceous fruits	23. Central Europe

TABLE 1. (Continued).

Subclass	Order	Family	Evidence	Geography	
Lower Eocene					
Asteridae	Gentianales	24. Apocynaceae	24. <i>Ochrosella ovalis</i> fruit	24. London Clay	
		25. Apocynaceae	25. <i>Ochrosoidea sheppeyensis</i> fruit	25. London Clay	
		26. Gentianaceae	26. <i>Pistillipollenites</i> pollen, floral	26. Northeastern Texas	
	Lamiales	27. Boraginaceae	27. <i>Ehretia ehretioides</i> fruit	27. London Clay	
		Solanales	28. Convolvulaceae	28. <i>Merremia tridentata</i> pollen	28. Cameroon
	Rosidae	Solanales	29. Solanaceae	29. <i>Cantisolanum daturoides</i> fruit	29. London Clay
			Euphorbiales	30. Euphorbiaceae	30. <i>Euphorbiospermum ambiguum</i> seed
		Fabales	31. Euphorbiaceae	31. <i>Euphorbiotheca minor</i> fruit	31. London Clay
			32. Caesalpiniaceae	32. <i>Caesalpinia</i> -type pollen	32. Assam
			33. Mimosaceae	33. <i>Mimosites browniana</i> bowerbank, fruit	33. London Clay
Myrtales		34. Lythraceae	34. <i>Minsterocarpum alatum</i> fruit	34. London Clay	
			35. <i>Pachyspermum quinquelocularis</i> fruit	35. London Clay	
		36. Myrtaceae	36. <i>Palaeorhodomyrtus subangulata</i> bowerbank, fruit	36. London Clay	
		Santalales	37. Onagraceae	37. <i>Palaeocharidium cellulare</i> fruit	37. London Clay
38. Loranthaceae			38. <i>Arceuthobium</i> -type pollen	38. North-central Europe	
Zingiberidae	Zingiberales	39. Loranthaceae	39. <i>Loranthus elegans</i> -type pollen	39. Germany	
		40. Cannaceae	40. Cannaceous leaves	40. Texas	
		41. Zingiberaceae	41. Zingiberaceous leaves	41. Texas	
Paleocene					
Asteridae	Gentianales	42. Apocynaceae	42. <i>Alyxia</i> -type pollen	42. Northwest Borneo	
		43. Gentianaceae	43. Gentianaceous pollen and associated floral type	43. Mississippi Embayment	
Rosidae	Euphorbiales	44. Euphorbiaceae	44. Inflorescences of the tribe Hippomane	44. Mississippi Embayment	

TABLE I. (Continued).

	Subclass	Order	Family	Evidence	Geography
		Fabales	45. Caesalpinaceae	45. <i>Crudia</i> -type pollen	45. Nigeria
			46. Caesalpinaceae	46. <i>Maniltoa grandiflora</i> -type pollen	46. Texas
			47. Mimosaceae	47. Flowers and inflorescences	47. Mississippi Embayment
			48. Papilionaceae	48. Flowers	48. Mississippi Embayment
		Myrtales	49. Myrtaceae	49. <i>Leptospermum</i> and <i>Metrosideros</i> -type pollen	49. a) New Zealand b) Ninetyeast Ridge
			50. Myrtaceae	50. <i>Syncolpites lisamae</i> pollen	50. Australia
		Polygalales	51. Polygalaceae	51. <i>Monnina</i> -type pollen	51. Chile
		Proteales	52. Proteaceae	52. <i>Adenanthus</i> -type pollen	52. Australia
			53. Proteaceae	53. <i>Banksia</i> -type pollen	53. Australia
			54. Proteaceae	54. <i>Beauprea</i> -type pollen	54. South Australia
			55. Proteaceae	55. <i>Symphyonema</i> -type pollen	55. Queensland
			56. Proteaceae	56. <i>Xylomelon</i> -type pollen	56. Australia
Cretaceous					
Stage					
Maestrichtian	Asteridae	Gentianales	57. Gentianaceae	57. Pollen associated with flowers	57. Northeastern Texas
Coniacian	Rosidae	Euphorbiales	58. Euphorbiaceae	58. <i>Paraphyllanthoxylon</i> wood	58. a) Arizona b) South Africa
Maestrichtian		Fabales	59. Caesalpinaceae	59. <i>Sindora</i> -type pollen	59. Siberia
Santonian		Myrtales	60. Myrtaceae	60. <i>Syncolporites lisamae</i> pollen	60. Gabon
Maestrichtian			61. Onagraceae	61. <i>Epilobium</i> -type pollen	61. a) California b) Brazil
Maestrichtian		Proteales	62. Proteaceae	62. <i>Helicia</i> -type pollen	62. California
Maestrichtian			63. Proteaceae	63. <i>Guevina</i> -type pollen	63. Northern South America/Central Africa
Upper Senonian			64. Proteaceae	64. <i>Guevina</i> -type pollen	64. New Zealand
Lower Senonian		Sapindales	65. Sapindaceae	65. <i>Cupanopsis</i> -type pollen	65. a) Gabon b) India
Maestrichtian	Zingiberidae	Zingiberales	66. Zingiberaceae	66. <i>Zingiberopsis</i> leaves	66. Wyoming, Colorado

TABLE 1. (Continued).

Upper Eocene	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
	1. Funnel or salverform, sympetalous corolla	1. Melittophily, Psycophily	1. a) Salard-Cheboldaeff (1978) b) Muller (unpubl. data)
	2. Funnelform, sympetalous corolla	2. Melittophily, Psycophily, Ornithophily	2. Krutzsch (1970)
	3. Brush-type flowers, often with tubular corolla	3. Chiropterophily, Melittophily, Ornithophily, Psycophily	3. Salard-Cheboldaeff (1978)
	4. As above ^c	4. As above	4. Salard-Cheboldaeff (1978)
	5. As above	5. As above	5. Salard-Cheboldaeff (1978)
	6. As above	6. As above	6. Salard-Cheboldaeff (1979)
	7. Trumpet-type flowers formed by prolonged hypanthium	7. Psycophily	7. Salard-Cheboldaeff (1978)
	8. Tubular flowers by an extended hypanthium, some brush-types	8. Chiropterophily, Melittophily, Ornithophily, Psycophily	8. Germeraad et al. (1968)
	9. Flowers pendent, with a prolonged hypanthium	9. Myophily, Ornithophily, Phalaenophily	9. Mildenhall (1980)
	10. Tubular and brush-type flowers	10. Melittophily, Ornithophily	10. Mildenhall (1980)
Middle Eocene	11. Sympetalous corolla, tubular, often bilabiate	11. Hymenoptera (wasp), Myophily, Ornithophily, Phalaenophily	11. Gruas-Cavagnetto (1978)
	12. Strongly irregular, sympetalous corolla, trumpet-type, often bilabiate	12. Chiropterophily, Ornithophily	12. Frederiksen (1973, 1977)
	13. Funnelform, sympetalous corolla	13. Myophily, Melittophily	13. a) Pares Regali et al. (1974a, 1974b) b) Legoux (1978)
	14. Tepals connate toward base	14. Hymenoptera (wasp), Myophily, Ornithophily	14. a) Chandler (1954) b) Manchester and Dilcher (1979), Crepet and Daghljan (1981b)
	15. Flag-type flowers, strongly irregular, not papilionaceous	15. Chiropterophily, Melittophily	15. Legoux (1978)
	16. As above	16. Chiropterophily, Melittophily, Ornithophily, Psycophily	16. a) Crepet and Dilcher (1977) b) Daghljan et al. (1980)
	17. As above	17. As above	17. Salard-Cheboldaeff (1978, 1979)
	18. Predominantly brush-type flowers	18. Chiropterophily, Ornithophily, Melittophily	18. Elsik and Dilcher (1974)

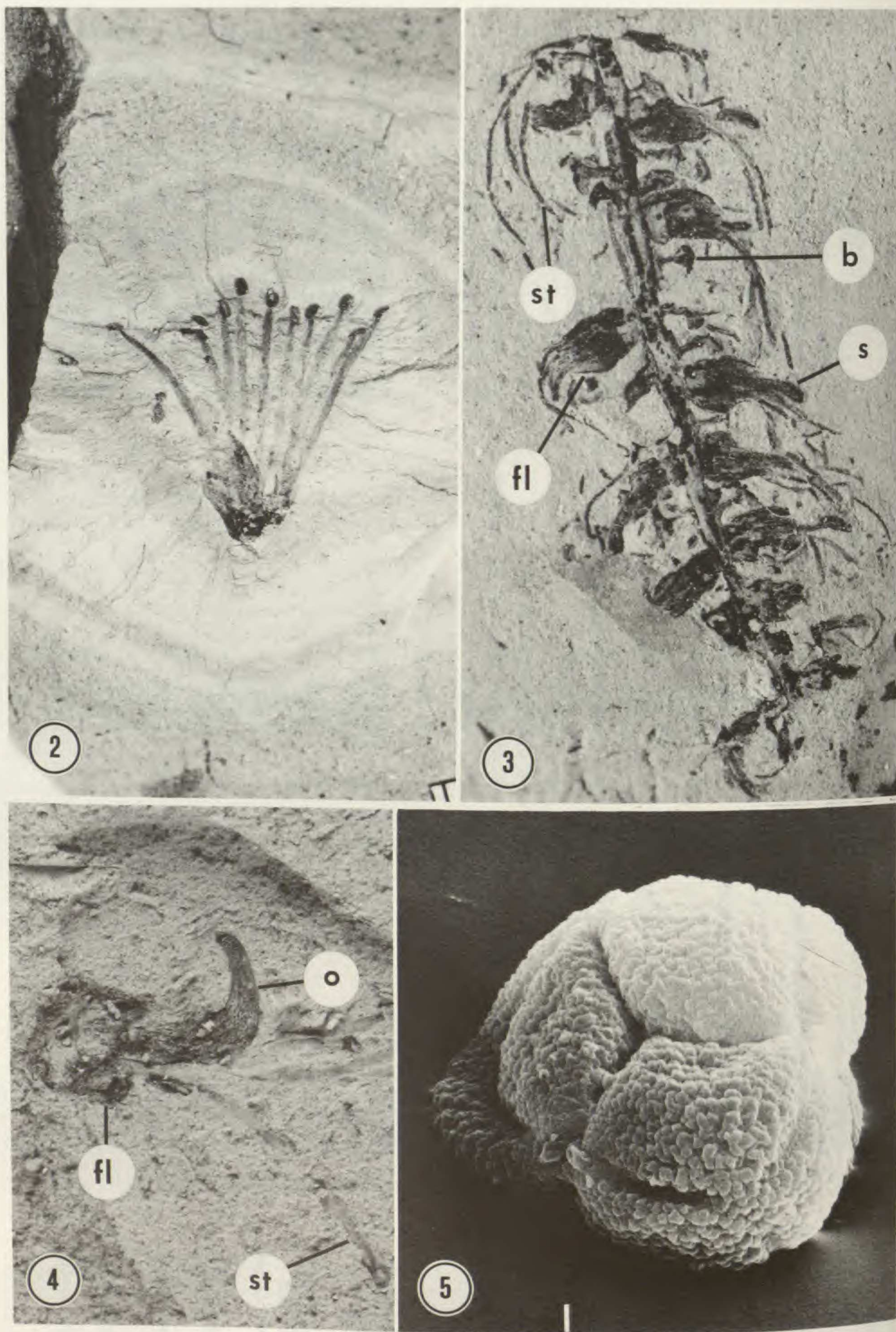
TABLE 1. (Continued).

	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
	19. Irregular, tending to zygomorphy	19. Melittophily	19. Pares Regali et al. (1974a, 1974b)
	20. Irregular, some flag-types	20. Melittophily	20. Kemp (1976)
	21. Strongly irregular, tubular corolla	21. Lepidoptera, Melittophily, Myophily	21. a) Crepet and Daghljan (unpubl. data) b) Trivedi and Verma (1971)
	22. Irregular, strongly nectariferous, briefly tubular	22. Chiropterophily, Ornithophily	22. Jain (1963)
	23. Zygomorphic, flag-type, tubular corolla	23. Melittophily, Ornithophily, Psychophily	23. Koch and Friedrich (1971)
Lower Eocene	24. As above	24. As above	24. Reid and Chandler (1933)
	25. As above	25. As above	25. Reid and Chandler (1933)
	26. Slender sympetalous corolla, bell- or trumpet-shaped	26. Melittophily, Psychophily	26. Crepet and Daghljan (1981a)
	27. Corolla generally salverform, sometimes tubular or funnellform	27. Melittophily	27. Chandler (1961)
	28. As above	28. As above	28. Salard-Cheboldaeff (1975)
	29. Various funnellform, tubular, trumpet-like flowers	29. Melittophily, Myophily, Phalaenophily, Chiropterophily	29. Reid and Chandler (1933)
	30. As above	30. As above	30. Reid and Chandler (1933)
	31. As above	31. As above	31. Reid and Chandler (1933)
	32. As above	32. As above	32. Baksi (1972, 1973, 1974), Sah (1974)
	33. As above	33. As above	33. Reid and Chandler (1933)
	34. As above	34. As above	34. Reid and Chandler (1933)
	35. As above	36. As above	35. Reid and Chandler (1933)
	36. As above	37. Melittophily, Myophily, Ornithophily, Phalaenophily	36. Reid and Chandler (1933)
	37. Funnelform to tubular flowers		37. Reid and Chandler (1933)
	38. As above	38. As above	38. Krutzsch (1970)
	39. As above	39. As above	39. Krutzsch (1970)
	40. Erect, tubular, highly irregular symmetry	40. Melittophily, Ornithophily, Psychophily	40. Daghljan (unpubl. data), Ball (1930), Berry (1916), Daghljan (1981)
	41. As above	41. As above	41. Daghljan (unpubl. data)
Paleocene	42. As above	42. As above	42. Muller (1968)
	43. As above	43. As above	43. Elsik (1968)

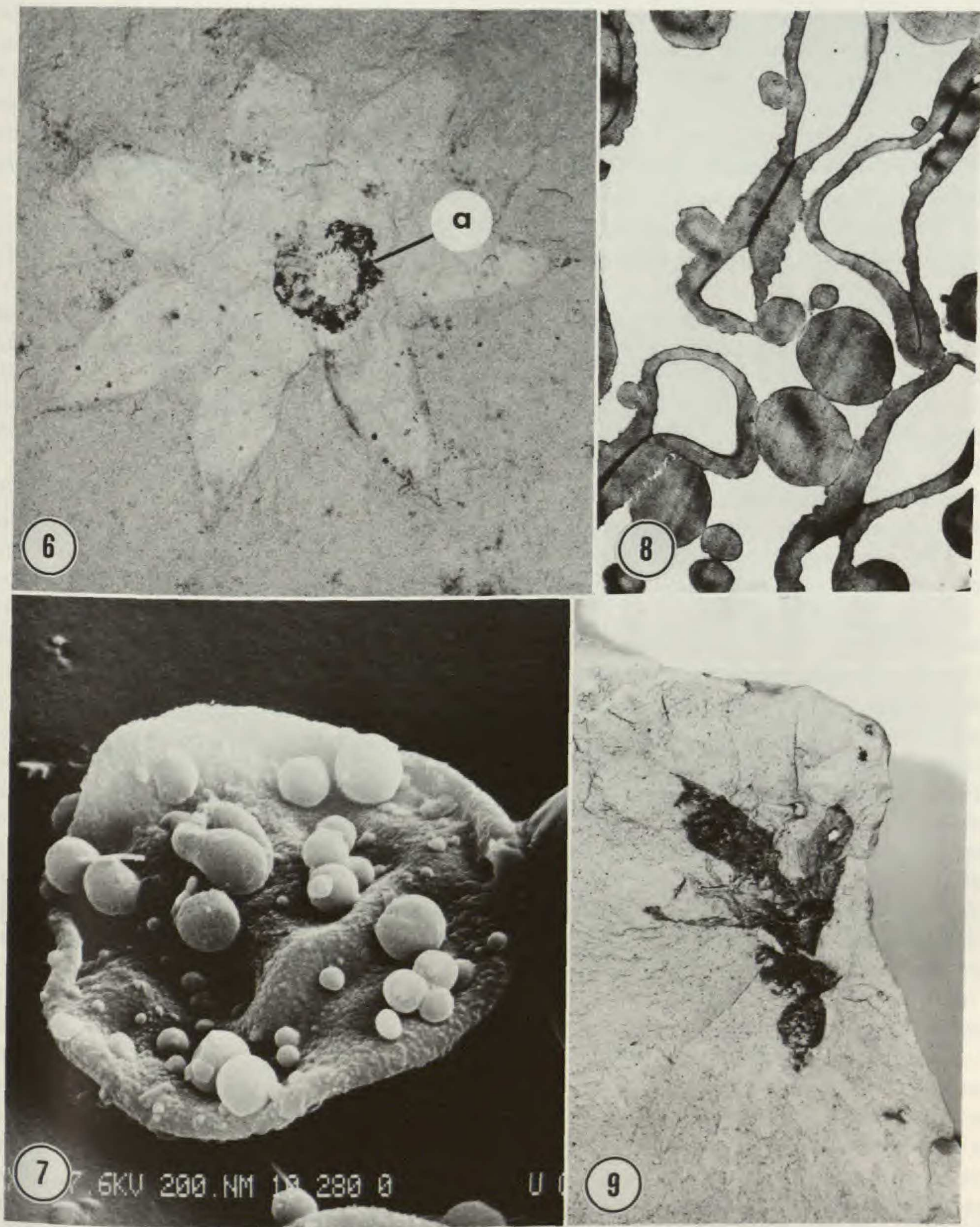
TABLE I. (Continued).

	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
	44. As above	44. As above	44. Crepet (unpubl. data)
	45. As above	45. As above	45. Adegoke et al. (1978)
	46. As above	46. As above	46. Elsik (1968)
	47. As above	47. As above	47. Crepet (unpubl. data)
	48. Papilionaceous zygomorphic flowers	48. Melittophily	48. Crepet (unpubl. data)
	49. As above	49. As above	49. a) Mildenhall (1980) b) Harris (1974)
	50. As above	50. As above	50. Harris (1965a), Martin (1978)
	52. Flag-type, strongly irregular symmetry	51. Melittophily	51. Doubinger and Chotin (1975)
	52. Brush-type flowers	52. Ornithophily (some mice and small marsupials)	52. Harris (1965a), Martin (1978), Stover and Partridge (1973)
	53. As above	53. As above	53. Martin (1978)
	54. As above	54. As above	54. Harris (1965a)
	55. As above	55. As above	55. Harris (1965b)
	56. As above	56. As above	56. Stover and Partridge (1973)
Cretaceous			
Stage			
Maestrichtian	57. As above	57. As above	57. Crepet and Daghljan (1981a)
Coniacian	58. As above	58. As above	58. a) Bailey (1924), Webster (1967) b) Madel (1962)
Maestrichtian	59. As above	59. As above	59. Van Campo (1963), Krutzsch (1969)
Santonian	60. As above	60. As above	60. Boltenhagen (1976a, 1976b)
Maestrichtian	61. As above	61. As above	61. a) Chmura (1973) b) Pares Regali et al. (1974a, 1974b)
Maestrichtian	62. As above	62. As above	62. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Maestrichtian	63. As above	63. As above	63. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Upper Senonian	64. As above	64. As above	64. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Lower Senonian	65. As above	65. As above	65. a) Belsky et al. (1965), Boltenhagen 1976b) b) Vinkatachala and Sharma (1974)
Maestrichtian	66. As above	66. As above	66. Hickey and Peterson (1978)

^a Subclasses are arranged alphabetically within each geologic time unit; their position within that unit is not indicative of their order of appearance.



FIGURES 2-5. 2. Brush blossom. $\times 2.5$. UCPC (University of Connecticut Paleobotanical Collection) B553. 3-5. *Eomimosoïdea plumosa*.—3. Inflorescence, note the floral envelopes (fl), style and stigma (s), stamens (st), and subtending bracts (b). $\times 5$. UCPC H45.—4. Floret with an expanding ovary (o). Note the floral envelope (fl), the stamens (st), and that the carpel is hairy. $\times 7$. UCPC W29.—5. Scanning electron micrograph of a tetrad of tricolporate pollen grains. $\times 2,500$.



FIGURES 6-9. 6. Flower with seven-parted sympetalous corolla. Note the compressed ring of anthers (a). $\times 3.2$. UCPC Ma322.—7. Scanning electron micrograph of pollen (when dispersed *Pistillipollenites macgregorii*) isolated from the flower illustrated in Figure 6. Note the gemmate processes. $\times 3,180$.—8. Transmission electron micrograph of pollen illustrated in Figure 7 illustrating the intectate wall structure, gemmate processes, and residual columellae under certain of the gemmae. $\times 5,800$.—9. Flower with a narrow floral tube. $\times 3$. IUPC (Indiana University Paleobotanical Collection) P2226.

specifically where lepidopteran pollination is also common (Weaver, 1972).

Pollen is particularly important because its unique nature makes its occurrence a reliable indication that the same taxon and thus, floral structure, is involved whenever it occurs. *Pistil-*

lipollenites macgregorii is known to extend into the Maestrichtian, suggesting that a pollination syndrome associated with bee pollination and, therefore, bees existed at that time. Surprisingly advanced Maestrichtian floral morphology may be an indication that bee pollination existed pre-

vious to that time. Pollen morphology provides additional corroboration for this assumption. Pollen with ornamentation similar to that of *P. macgregorii* is found in four extant taxa (Nowicke & Skvarla, 1974; Nilsson, 1970; Poole, 1981). In two of these families (Gentianaceae, Euphorbiaceae), variation in pollen is sufficiently well known that the sequence of evolution leading to gemmate pollen can be reconstructed (e.g., Nilsson, 1970). In each case gemmate, intectate pollen results from a breakdown of the muri of reticulate pollen accompanied by the elaboration of the tectum in localized areas. The progression suggests that gemmate pollen is a derived type and likely to be the end product of an evolutionary lineage; possibly one that originated previous to the Maestrichtian.

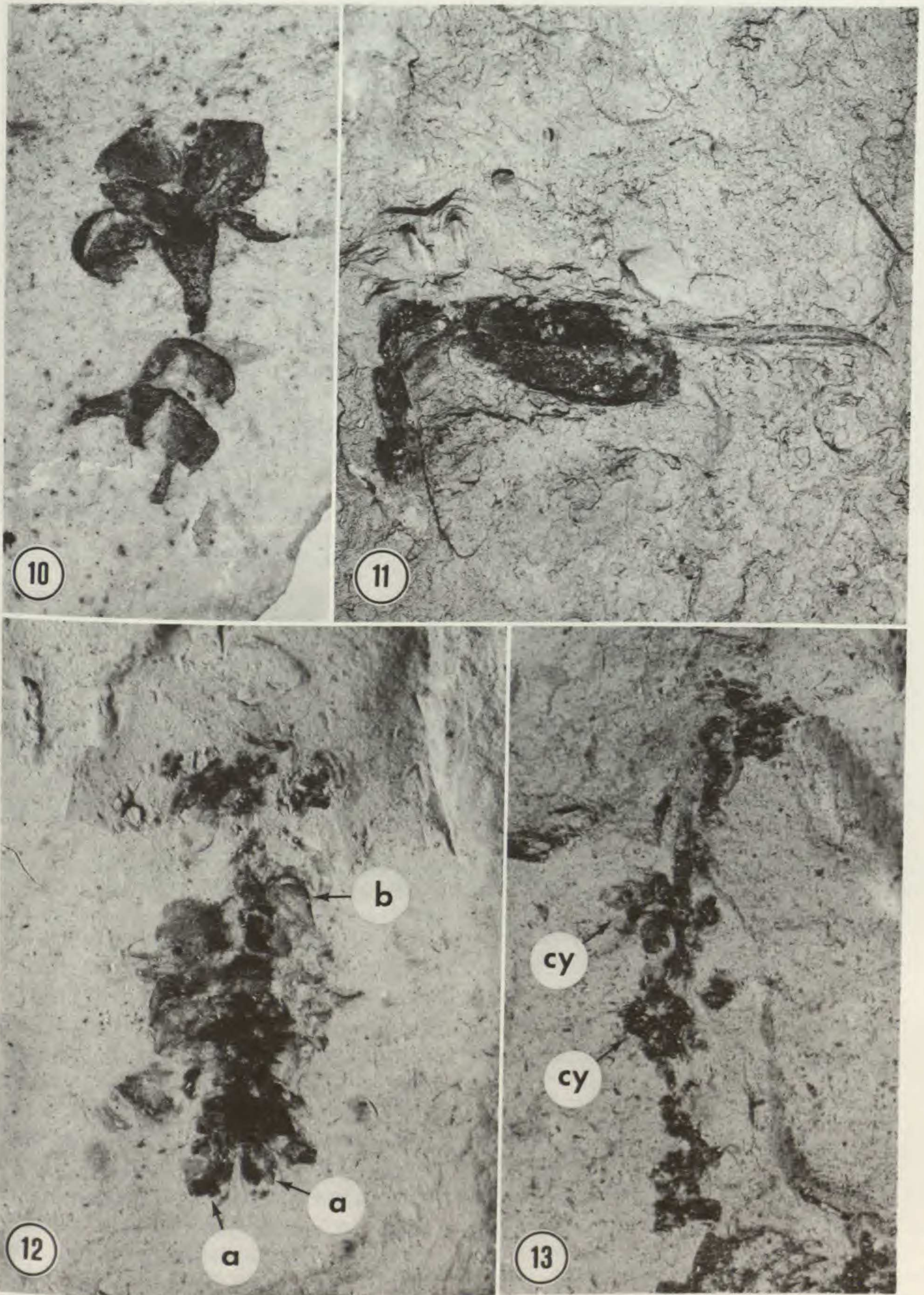
Sympetalous, funnellform-salverform flowers of as yet unknown affinities that have floral tubes narrow enough to suggest lepidopteran pollination (Figs. 9, 10) exist in Middle Eocene sediments of both the Green River Formation and the Claiborne Formation. In these cases the flowers also appear to be radially symmetrical, suggesting probable butterfly, as opposed to moth, pollination.

Zingiberidae. The taxa composing the Zingiberidae are remarkable for their often radical zygomorphy and their adaptations to a variety of advanced pollinators, including bees. Despite the derived nature of the flowers of this taxon, the Zingiberidae seem to be remarkably advanced by the Eocene. Fruits provide some of the most compelling data on the status of the group at this time. The Musaceae have been reported from the Eocene Deccan Intertrappean Series (Jain, 1963) and fruits of the Zingiberaceae have been reported from Eocene through Miocene sediments (Koch & Friedrich, 1971). Due to the highly adapted nature of zingiberidean flowers it has been suggested that floral structure in Paleogene taxa might have been different from floral structure in modern species (Daghlian, 1981). In view of the modern nature of the Paleogene fruits and the close relationship between fruit and flower structure, it seems more likely that they had flowers similar to those of modern taxa. This possibility is supported by a recently discovered zingiberidean flower (Fig. 11), from the Claiborne Formation (Middle Eocene). Although still in preliminary stages of investigation, this flower seems to be closest to the modern Heliconiaceae.

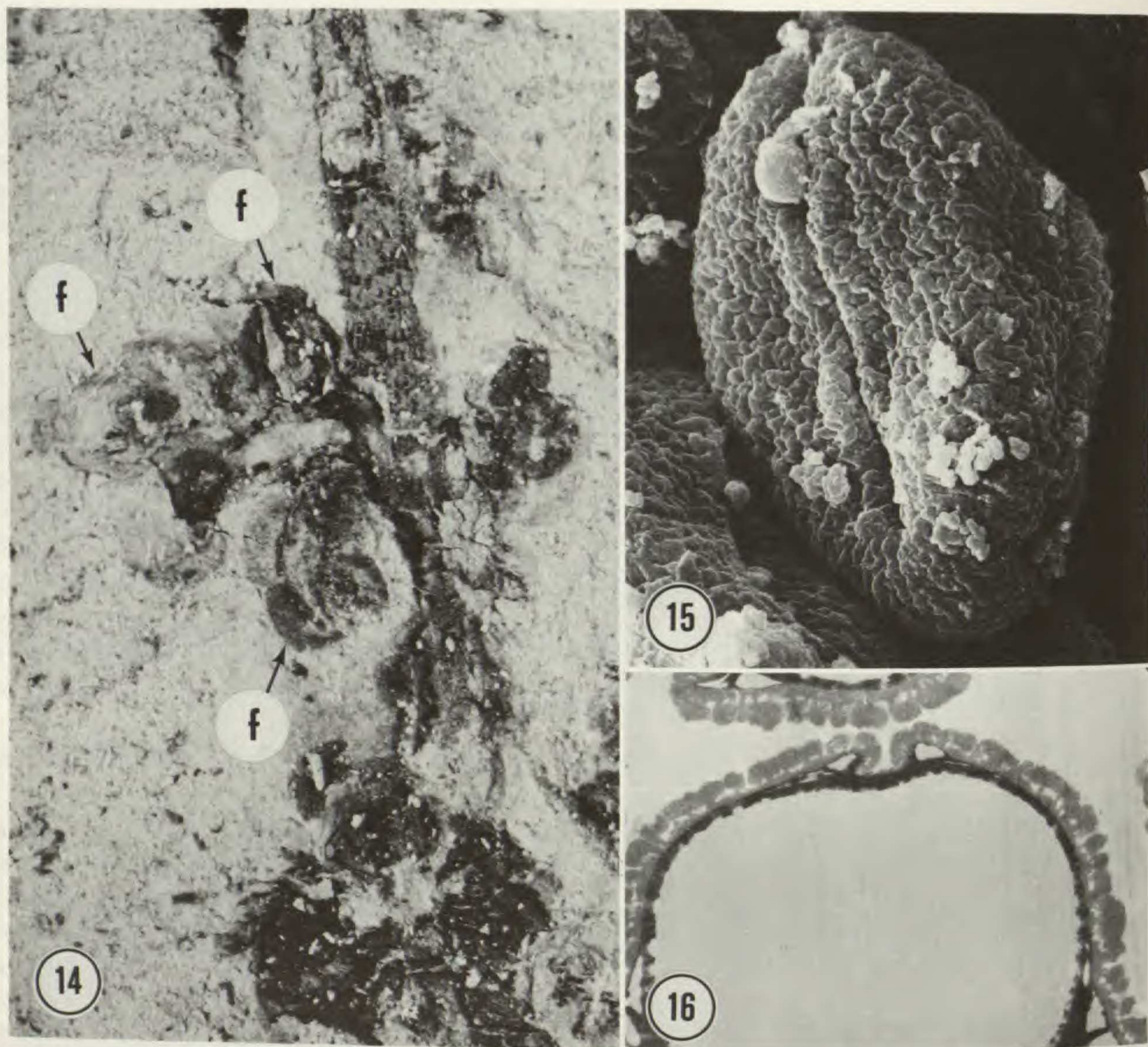
One of the most exciting recent developments relating to monocot history has been the discovery of zingiberalean leaves of Maestrichtian age. These are well documented and suggest the presence of highly advanced pollination syndromes during the Maestrichtian (Hickey & Peterson, 1978).

Euphorbiaceae. The Euphorbiaceae are one of the largest families of flowering plants and one in which diversity has been associated with adaptation to a wide range of insect pollinators (Stebbins, 1981). The state of the Euphorbiaceae by the Middle Eocene is a good indication of the rapidity of radiation of pollination mechanisms associated with insect pollination. The number of discrete fossil euphorbiaceans is small, but their nature makes it possible to infer something of the history of the family. Fruit and flower fossils of Middle Eocene age reveal that one of the most advanced tribes of the Euphorbiaceae, the Hippomane, was diverse and essentially modern by the Middle Eocene. Fruits reported by Manchester and Dilcher (1979) suggest that taxa similar to the hippomanean genera *Hippomane* and *Hura* were extant at that time. Inflorescences provide corroboration that this extremely derived tribe was modern by the Middle Eocene (Crepet & Daghlian, 1981b). Inflorescences were preserved at two ontogenetic stages: before the cymules expanded while the florets were still partially enclosed by a subtending bract (Fig. 12) and at maturity (Fig. 13). Inflorescences are sometimes branched spikes of cymules. Each cymule is composed of at least three staminate florets with at least three anthers each and is subtended by an ovate, cupped bract (Figs. 12, 14). Pollen is tricolporate and prolate with longitudinal pores (Fig. 15). Exine is tectate columellate and perforate (Fig. 16). Ornamentation is interesting because the convoluted reticulum has striate muri. Inflorescence, cymule, and pollen morphology are similar to those of the genera *Gymnanthes* and *Senefeldera* in the Hippomane (Crepet & Daghlian, 1981b). The appearance of such modern taxa by the Eocene suggests an earlier origin for the family. This is supported by reliable reports of Cretaceous woods similar to those of certain modern genera (Webster, 1967) and by recently discovered Paleocene hippomanean inflorescences (Crepet, unpubl. data).

What is known of the history of the Euphorbiaceae gives the general impression (consistent with other paleobotanical data) that there was



FIGURES 10-13. 10. Another type of flower with a narrow corolla tube. $\times 3$. UCPC G399.—11. Flower of the Zingiberidae. $\times 2.3$. UCPC 520.—12. Part of an immature inflorescence of *Hippomaneioidea*. Note the cup-shaped bract (b) and the anthers (a) protruding from another bract. $\times 7.75$. UCPC W14.—13. A mature inflorescence of *Hippomaneioidea* showing the expanded cymules (cy). $\times 4.3$. UCPC W55.



FIGURES 14–16. *Hippomaneioidea*.—14. Higher magnification view of UCPC W55 showing two expanded cymules—one compressed laterally and one compressed in face view. Note that the laterally compressed cymule is composed of at least three florets (f) of 3–4 anthers each. $\times 16$.—15. Scanning electron micrograph of pollen isolated from UCPC W55. $\times 2,500$.—16. Transmission electron micrograph of pollen isolated from UCPC W55 illustrating the tectate-columellate wall structure. $\times 4,800$.

relatively early (Upper Cretaceous—early Paleogene) radiation associated with insect pollinators.

SUMMARY OF PALEOBOTANICAL EVIDENCE

Evidence based on carefully investigated organ taxa including flowers and inflorescences suggests that families with pollination syndromes reflective of pollination by Apoidea and Lepidoptera existed by the Middle Eocene. Such advancement indicates an earlier radiation of pollination mechanisms involving faithful pollinators. The earlier Paleogene and Upper Cretaceous records are consistent with this possibility (Table 1) and the nature of pollination syndromes associated with families that occur during the Maestrichtian suggests that co-evo-

lutionary relationships between angiosperms and faithful pollinators began at an earlier time. It is risky to suggest that the appearance of an advanced taxon at a given time implies a lengthy previous history. The projection of speciation models into geologic time by Eldredge and Gould (punctuated equilibria, 1972) and their consistency with angiosperm reproductive biology and the angiosperm fossil record (Crepet, 1982) introduces the possibility that the appearances of relatively modern syndromes at particular times are the culminations of events initiated just prior to their appearances in the fossil record. Nevertheless, the complexity of plant-pollinator interactions and the involvement of co-evolution in their origin do suggest that advanced pollinators, at least at higher taxonomic levels, e.g., superfamily Apoidea, may even have existed earlier

than the uppermost Cretaceous, even if their evolution proceeded as in the punctuated equilibrium model.

EVOLUTIONARY HISTORY OF FAITHFUL POLLINATORS

The two most important groups of pollinators in terms of promotion of speciation are the Apoidea, and to a slightly lesser degree, Lepidoptera. The discussion of advanced pollinators is consequently directed primarily toward these two groups. Coleoptera and Diptera are certainly important pollinators but do not have the ethologies associated with heightened promotion of speciation events. Both orders were well developed during the entire Mesozoic, especially the Coleoptera, and perhaps both were important in the establishment of basic angiosperm floral features. They undoubtedly contributed to Early Cretaceous radiation and spread of the angiosperms. Birds and bats are also important pollinators; however, they are not numerically as significant as insects, and birds tend to be promiscuous pollinators (Stiles, 1981), while fidelity in bats is poorly understood (Koopman, 1981). However the history of bats and birds suggests that neither were important pollinators until late Paleogene times (see review by Tiffney, 1984).

APOIDEA

It is interesting to examine data on the pattern of evolution of the Apoidea and to contrast these with the inferences obtained from the fossil record of plants. Although the most obvious place to begin is the fossil record of bees, that record is limited and most insights into the pattern of their radiation have been gained from a careful consideration of biogeography in light of their neontological features, including behavior, level of sociality, nesting habits, etc. (Michener, 1979).

The earliest record of fossil bees is either Eocene or Oligocene depending on the interpretation of the age of the Baltic amber. A diversity of fossil bees from various localities occurs at the same time including derived and ancestral tribes and subfamilies (by the Oligocene the Halictinae, Andreninae, Ctenoplectrinae, Melittinae, Anthidiini, Megachilini, Xylocoopini, Anthophorini, Meliponinae, Bombini, and Apini are known) (Michener, 1979). The presence of two of the four tribes of the Apidae by the Oligocene, including one of the two most highly derived tribes of extant bees (the Apini and Meliponini) is an in-

dication that bee origin may have occurred considerably earlier than the Oligocene. Certainly, the known fossils do not help to unravel the pattern of evolution in bees. The strongest evidence related to the antiquity of the Apoidea comes from the interpretation of their disjunct distributions.

Michener (1979) noted that the distributions of most present day bees are probably the result of slow spreading over continents and presently moderate barriers, since most bees are not good dispersers. Most bees do not fly during bad weather, so they are not likely to be dispersed by storm winds and most bees have a tendency to return to their nesting sites. Dispersal is even more restricted in highly social bees due to their mode of colony establishment. Thus, there are certain groups of bees whose disjunct distributions are best explained by continental movements or by dispersal across oceans at a time when they were relatively narrow.

The Colletidae. The Colletidae are a family of short-tongued solitary bees and are considered the most primitive family of extant bees on neontological grounds (important primitive features include bifid glossae similar to those of the sphecoid wasps and methods of carrying pollen, i.e., in the crop in two subfamilies (Hylaeinae and Euryglossinae) rather than on body hairs or more specialized structures (scopae; Michener, 1979; Thorp, 1979)). One tribe in particular has a distribution most easily accounted for by continental movements—the Paracolletini. These are presently restricted to temperate parts of three southern continents (Australia, Africa, and South America). Michener (1979) suggested that this disjunction may extend to the Upper Cretaceous when oceanic gaps were narrower. The colletids are an unusual family of bees inasmuch as in Australia, where they are most diverse, they are strongly associated with pollinating one particular family of angiosperms—the Myrtaceae. The presence of myrtaceous pollen in the Santonian (Table 1) supports Michener's suggestion.

The Fideliidae. The most primitive family of long-tongued bees, the Fideliidae, are closely related to the Megacheilidae (they are apparently sister groups, Michener, 1974). They are ground-nesters and particularly poor candidates for dispersal for that reason (i.e., flotation is out as a means of dispersal). Two species live in arid western South Africa and one is native to arid central Chile. Michener (1979) pointed out that the last direct migration route was closed in the

lower Upper Cretaceous and that it would have been inaccessible to these bees anyway, because it was through the tropics. He concluded that the family had a distribution during the Upper Cretaceous and dispersed across oceans that were narrower than at present.

The Meliponini. One of the most important indicators of apoidean antiquity is the present distribution of the Meliponini. They are particularly important due to their phylogenetic status, their degree of eusociality, and their inability to disperse. The best biogeographical evidence involves the subgenera of the genus *Trigona* (Michener, 1979). The Meliponini are as highly social as the Apini, and, together with the Apini, represent the most derived bees. The discovery of a genus as modern as *Trigona* in the Upper Eocene-Oligocene Baltic amber suggests an earlier origin for the family. In fact, the distribution of the modern subgenera of *Trigona* is explicable only by a mid-Upper Cretaceous origin of the subgenera. Before considering the details of their distribution, it is instructive to examine the features that make the Meliponini particularly bad dispersers. As highly eusocial bees, they are dispersed by swarms and not individuals. Swarms are so highly organized that Michener (1979) considered it impossible for them to cross sizable bodies of water. Even the pattern of swarming mitigates against dispersal. Individuals from a parent colony go back and forth to provision the new nest before the queen migrates. The apparent isolation of species and subspecies in Brazil by rivers (Michener, 1979), and the absence of meliponines from the Antilles, even though these islands are relatively close to major continental populations, represent good evidence for their lack of dispersability.

Despite these difficulties, the genus *Trigona* is worldwide in its distribution with similarities at the subgeneric level between South American taxa and those of all other southern continents except Antarctica. There are three disjunctions in poorly dispersing subgenera as follows:

Plebeia: found in American tropics, Australia, and New Guinea.

Tetragona: American tropics, the oriental region, and Australia.

Hypotrigona-Trigonisca: American tropics, Africa, and the oriental region.

In view of their inability to traverse even rather insignificant bodies of water, Michener (1979)

proposed that the principal subgenera of *Trigona* originated in the Middle or Upper Cretaceous when Africa and South America were joined or not yet widely separated at tropical latitudes.

LEPIDOPTERA

The fossil record of the Lepidoptera is better than that of the Apoidea, but it is still far from complete. Nonetheless, certain important aspects of the history of the Lepidoptera are evident from the fossil record.

The first reliable report of the Lepidoptera is based on several moths preserved whole in 100–130 Ma amber. These are related to the extant Micropterigidae (Lepidoptera, Zeugloptera; Whalley, 1977). Even though these fossils are the first evidence of the Lepidoptera, they are well defined micropterigids and are similar to the modern genus *Sabatinca*. Whalley (1977) proposed an origin for the Lepidoptera in the Jurassic based on the specialized nature of these fossils. Micropterigids are considered to be ancestral based on neontological features (Common, 1975) and are interesting because they have well-developed mandibles and no proboscis. Thus, it appears that the earliest lepidopterans were pollen feeders, if not predacious, and not nectar feeders.

There are several other reports of Cretaceous Lepidoptera in amber. One is of the head of a ditrysian larva from 73 Ma, another is of micropterigid scales from 100 Ma (Mackay, 1977; Kühne et al., 1973). In general, reports of Cretaceous Lepidoptera are rare, but what information is available provides an idea of their time of origin and degree of diversification (Monotrysia and Ditrysia are differentiated by the Upper Cretaceous).

A variety of fossil lepidopterans are known from the Paleogene, including one monotrysian moth, 41 ditrysian moths, and 27 butterflies (Durden & Rose, 1978). Perhaps the most interesting of these are three papilionid butterflies known from the Middle Eocene Green River Shale.

A variety of lepidopterous taxa are known from the later Tertiary and most are similar to their modern counterparts (Common, 1975). Common (1975), in his review of the fossil record of the Lepidoptera, concluded that the haustellate Lepidoptera were well established in the Cretaceous and that it is likely that the simple proboscis had evolved by the time angiosperms ap-

peared. He further assumed that the radiation of ditrysian forms paralleled that of the angiosperms. These seem to be reasonable assumptions based on the fossil record. Lepidoptera occur relatively early and ditrysian forms (i.e., usually with a proboscis) occur at least by 73 Ma. Further, a variety of Lepidoptera are present in the Paleogene, including the highly specialized Papilionidae. It seems more than likely that advanced lepidopteran pollinators were available during the Upper Cretaceous.

PATTERNS OF ANGIOSPERM DIVERSIFICATION

The tempo of angiosperm diversification is an essential datum in assessing the possibility of a relationship between advanced faithful pollinators and angiosperm diversity. Until recently (Niklas et al., 1980; Muller, 1981; Tiffney, 1981), there has been no really rigorous attempt to chart the course of angiosperm diversification. The notions that angiosperms arose *de novo* as modern taxa and almost instantaneously became dominant have been debunked by Doyle and Hickey (1976), but the angiosperms have been considered generally to be dominant worldwide by the lower Upper Cretaceous (e.g., Raven & Axelrod, 1974). Recent analyses of angiosperm diversity through time have presented a different picture.

Niklas et al. (1980) have analyzed angiosperm diversification based on reports of various fossil organs in the literature as part of their general survey of patterns of diversification in vascular plants. The results suggest that angiosperm diversity increased slowly and steadily during much of the Cretaceous with angiosperms becoming locally dominant during the Upper Cretaceous and achieving world dominance by the uppermost Cretaceous or Early Tertiary (Niklas et al., 1980). They provide a well thought out discussion defending their use of fossil species as the basis for their diversity curves, and in context (Niklas et al., 1980), species are clearly the fossil taxon of choice. One of the justifications for using fossil species involves inherently greater subjectivity in the designation of higher taxonomic levels. This may be true for higher taxonomic levels that are extinct and it is certainly true in extant taxa, but with fossil angiosperms there are reasons why higher taxonomic levels, particularly the family, may be superior indices of actual diversity. First and perhaps most important, families can be identified with great confidence in the fossil record. This provides an element of

reliability and eliminates inevitable distorting redundancy associated with the use of form taxa. Second, the biological validity of angiosperm families can be assessed on the basis of neontological data, since these families exist in the present as well as in the past. Third, using appearances of families as indices of diversity minimizes aberrations that might be associated with having relatively few megafossil localities at certain times. Finally, dominant angiosperm diversity is the result, not only of having certain extremely large families and genera, but predominantly, of having a great number of families. In fact, the average number of species/family in the angiosperms is comparable with the species/family ratio in gymnosperms (Stebbins, 1981). Thus, rate of appearances of families is a reasonable index of angiosperm diversification. Naturally, it is a compromise inasmuch as some diversity is masked, especially diversity preceding the origination of modern families.

Muller recently provided an account of the diversification pattern of angiosperm families based on his analysis of the palynological literature (1981). Muller's analysis is attractive because criteria for accepting or rejecting data on the occurrences of particular families are clearly discussed and because pollen has proven taxonomic value. Muller's analysis (1981) parallels that of Niklas et al. (1980) in illustrating a steady rise in total angiosperm diversity during most of the Cretaceous, but reveals a slightly earlier (Campanian) and more dramatic peak in diversification that reaches a maximum during the Maestrichtian and extends into the Paleogene. Interestingly, diversification patterns for orders and superorders, which would presumably include most angiosperms left out in a consideration of only modern families, are very similar to the pattern of diversification based on families alone (Muller, 1981).

Both analyses of angiosperm diversity are valuable attempts to clarify a pattern that has been predominantly subjectively interpreted. Both have their strengths and weaknesses, but in each instance the major dramatic radiation of angiosperms is revealed at a date later than has commonly been supposed.

SUMMARY OF DATA

1. Families having flowers adapted for pollination by Apoidea and Lepidoptera probably existed during the uppermost Cretaceous. The taxa

present at that time indicate a probability of earlier co-evolution of angiosperms with apoidean and lepidopteran pollinators.

2. Rigorous analysis of the biogeography of bees suggests that at least three families of the Apoidea were present by the uppermost Cretaceous; the Colletidae, Fideliidae, and Apidae. The Apidae were so well developed by that time that it is likely that three subgenera of the genus *Trigona* already existed.

3. The fossil record of the Lepidoptera indicates an origin for the order previous to 100 Ma with both monotrystian and ditrystian forms present by the Upper Cretaceous.

4. Angiosperm diversity increased steadily during the lower and part of the upper Cretaceous. They may have commenced a major diversification as early as the Campanian, but were certainly experiencing a major radiation by the Cretaceous-Tertiary boundary that continued into the Tertiary.

CONCLUSIONS

It is not reasonable at the present time to attempt to attribute angiosperm success to any single characteristic. In fact, many of the features of angiosperms that have been discussed by Stebbins (1981), Burger (1981), and Mulcahy (1979) have undoubtedly significance in angiosperm supremacy. Nonetheless, data on the progression of evolution of insect pollination mechanisms in angiosperms suggest that the inception of advanced insect pollination syndromes was either coincident with, or just prior to, a major radiation of flowering plants. Advanced insect pollination can no longer be excluded on the basis of paleontological evidence from having participated in a major radiation of angiosperms. On the contrary, paleontological data are consistent with neontological evidence in suggesting an important role for advanced insect pollinators in establishing contemporary angiosperm diversity.

There were undoubtedly several milestones in the evolution of angiosperm pollination mechanisms during the Cretaceous and Paleogene other than the appearance of advanced faithful pollinators, and these also must have affected angiosperm diversity. What can be inferred from the fossil record at the present time suggests the following sequence of events in the evolution of angiosperm pollination mechanisms:

1. The origin of insect pollination. Angiosperm origin involved co-evolution with insect

pollinators (dipteran or coleopteran) that resulted in the ancestral angiosperm flower. The first angiosperms had features conducive to successful radiation, including a truncated life cycle, enclosed ovules, insect pollination, and gametophytic competition (Stebbins, 1981; Doyle & Hickey, 1976; Burger, 1981). Evidence for the early predominance of coleopteran/dipteran pollination in angiosperms is provided by the fossil record, which illustrates the existence of all major magnoliidan pollen types during the Aptian/Albian (Zavada, unpubl. data).

2. During the mid-Cretaceous, wind pollination evolved in angiosperms possibly as a result of the combination of seasonally dry tropical-subtropical environments and competition for insect pollinators (Whitehead, 1969; Crepet, 1981). These taxa were pre-adapted to invade subsequent appropriate habitats, including those created by climatic decay.

3. The appearance of advanced faithful insect pollinators in the Upper Cretaceous/Paleogene.

4. The origin of bat and bird pollinators. These pollen vectors probably became significant no earlier than the mid-Paleogene (e.g., Stiles, 1981; Koopman, 1981; Tiffney, 1984) and, while certainly contributing to angiosperm diversity by increasing the adaptive space associated with animal pollination, they are not as significant numerically as insect pollinators.

5. Finally, the ultimate refinements of the specific plant-pollinator interaction (e.g., the Orchidaceae) and of the non-specific plant pollinator interaction (e.g., the Compositae; Proctor, 1978). These alternative developments must have occurred late in the Tertiary, but there is little germane fossil evidence at this time.

Regal (1977) has pointed out the possibility that synergism between insect pollinators and animal seed dispersal vectors may have been important in the major radiation of angiosperms (although his timing was way off due to his apparent unfamiliarity with such things as the nature of pollinating vs. non-pollinating Hymenoptera, etc.). A modification of this proposal, i.e., that *faithful* insect pollination and animal seed dispersal vectors were of utmost importance in maximizing angiosperm diversification during the uppermost Cretaceous-Lower Tertiary, remains a viable and even exciting possibility (consider the present chapter in conjunction with that of Tiffney, 1984). Animal dispersal maximizes the probability that, given a heterogeneous terrestrial biospace, a small population will be iso-

lated in a new environment (Tiffney, 1984; see discussion also by Vrba, 1980, fig. 1C). Constant pollinators, stochastic floral change, and animal seed dispersal vectors may interact in a variety of ways to further promote speciation (Fig. 1A–C). Because these elements of angiosperm reproductive biology are conducive to the stochastic isolation of small populations and because of the apparent importance of stasis in angiosperm history (Crepet, unpubl. data), I consider the punctuated equilibrium model of evolution to have merit with regard to the angiosperms. Differences in the timing of events; i.e., the coincidence of the appearance of advanced insect pollination mechanisms with the onset of the major angiosperm radiation during the Campanian according to Muller (1981), versus a slightly later date for maximal angiosperm diversification as reported by Niklas et al. (1980) and Tiffney (1981), are probably not significant given the constraints imposed by the degree of resolution presently available from the fossil record. What is important is the understanding that presently available fossil data do show an uppermost Cretaceous–Early Tertiary and not an earlier peak in angiosperm diversification rate.

It now appears that the inception of advanced pollination mechanisms preceded widespread animal seed dispersal (Tiffney, 1984). If future investigations bear out this possibility, it will suggest advanced insect pollination alone might have been responsible for the onset of a major angiosperm radiation while synergism with animal seed dispersal vectors became an important factor at a slightly later time.

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